

AN EXPERIMENTAL STUDY OF THE REPRODUCTIVE
HABITS AND LIFE HISTORY OF THE CICHLID FISH,
AEQUIDENS LATIFRONS (Steindachner)

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INTRODUCTION

Although the reproductive habits of a large number of cichlid fishes have been described in various publications, the bulk of them have appeared in journals devoted to home aquaria and for most part are uncritical and concerned entirely with fish cultural interests. These fishes, with their highly specialized reproductive behavior, nevertheless recommend themselves strongly to the experimentalist. The present contribution is an attempt to analyze the more evident and basic of the elements involved in the breeding habits and life history of one member of the family Cichlidae, namely, *Aequidens latifrons* (Steindachner). Although this species is well known to aquarists and is mentioned in practically every list of small fishes, the writer has been unable to find a single paper devoted to a critical study of the behavior of this fish. Most briefly describe the aquarium habits of *A. coeruleopunctata* or *latifrons* and are essentially in agreement with the present studies in the general aspects. Engmann (1907) gives the most elaborate early discussion. The others, largely short notes, are not of sufficient bearing on the present study to warrant inclusion in the bibliography. Most recently, Schoenebeck (1933) considers the entire family, at considerable length, from the aquarists' viewpoint. Coates (1932) discusses in general terms the behavior of the parents of the fishes used for the present series of experiments.

As is well known, the cichlids either attach their eggs to some solid support and guard them, or carry them about in the mouth. The first and most common method is certainly the most

primitive. The egg-carrying habits of such genera as *Haplochromis* and *Tilapia* can only be considered a specialized development, as will be subsequently shown. Aside from this difference there is no outstanding change from one species to another in each group, so far as known, all following a general pattern with minor variations. The species considered herewith may serve as a typical representative of the more primitive group.

The fishes on which these studies were made are the aquarium-bred offspring of some specimens collected in 1931 by Mr. A. Eisinger at Barranquilla, Colombia. These fishes were brought to the New York Aquarium while still very small and as they grew up in aquaria their behavior appeared to be entirely normal, especially as compared with field observations made in 1924 on the questionably distinct *Aequidens coeruleopunctatus* (Kner and Steindachner) in Panama. Such details that could be seen under field conditions agree closely with those studied subsequently in the laboratory. Throughout the laboratory studies, helpful assistance was rendered by C. W. Coates of the Aquarium staff. The photographs were all made by S. C. Dunton, also of the Aquarium, excepting Figs. 5, 6A and 8A which are the author's.

The following sections discussing the details of behavior are presented, so far as possible, in chronological order, beginning with the young fish just after they have escaped the parental influence. Part of this is naturally of the simple observational procedure but is reinforced wherever possible by definite experimental work, which is so stated and explained at its place of occurrence, together with such discussional remarks that may pertain.

HABITS OF THE YOUNG FISH

When the young fish attain a sufficient size, the juvenile schooling reaction disappears and is replaced by some centrifugal influence causing the individuals to scatter. They then no longer seek one another's company and all comers appear to be unwelcome. At this time fighting appears but usually proceeds little beyond a chase and a single nip. Concomitantly with this change in behavior, or a little prior to it, the adult pattern and

coloration begin to appear, so there is reason to suppose that these changes in behavior are basically dependent on the developing gonads, or at least on changes in the endocrine complex foreshadowing sexual maturity.

As the parent fish in a state of nature may be seen in attendance on fishes at least 30 mm. long, and maturity is reached under such circumstances at a length of about 70 mm., it follows that the time between the schooling habit period and the full development of the adult behavior is not long and would be, presumably, an abrupt rather than a gradual one.¹ This is fully borne out by aquarium observations. In fact in the relatively close confines of an aquarium, it is sometimes difficult to decide when the juvenile school has broken up and courtship has begun. Maturity not infrequently occurs at smaller sizes in aquaria so that some individuals of one brood may actually be breeding while less precocious ones still show the last remnants of the juvenile schooling habit. A typical adult pair is illustrated in Fig. 4, and the young, at about the time they escape the parental solicitude but before they begin to take on adult coloration, in aquarium-reared material, are shown in Fig. 11B.

HABITS OF THE ADULT FISH

The behavior of the non-breeding but fully mature fish is very definite and all of its characteristics have been foreshadowed in the later stages of the family school. With the complete disappearance of the latter the fishes tend to become solitary and will fight, sometimes disastrously, with all of their own kind including both sexes, and not infrequently with other species, especially if they somewhat resemble themselves. Crowding emphasizes the fighting reaction to such an extent that the quarrels may almost be considered a direct function of the size of the aquarium up to a certain point beyond which the crowding seems to inhibit fighting on the basis of confusion. This fact is readily understood when considered in the light of the known behavior of a considerable variety of fishes. It is naturally evident chiefly in fishes that display a non-schooling reaction. Many such fishes

¹ Based on field observation of *Aequidens coeruleopunctatus*. See Breder (1927).

under feral conditions establish a kind of property right about some retreat or area, and join battle with any intruder that may so much as swim near the site. This behavior is especially notable about coral reefs where such a variety as *Xyrichtys*, *Abudefduf*, *Pomacentrus*¹ and *Gnathypops* may serve as illustrations, although such behavior may be found in other localities, both fresh and salt. In some species it appears only as a part of the reproductive behavior and then relates only to the nest area (e.g. *Lepomis*, *Boleosoma*, *Cyclopterus* and *Ameiurus*). The behavior in general terms appears to be analogous to the well known breeding and feeding areas of birds, especially as fighting does not normally occur in "neutral" territory. Even if two fish go for the same piece of food, the loser simply retreats. In the present species this phenomenon becomes more and more prominent with the development of the gonads.

It so happens that the regions in which *Aequidens* lives are subjected to rather protracted dry seasons. It is consequently not uncommon, at times, for the fishes to become concentrated in pools in the stream beds to an annoying degree (See Breder, 1927). Of course sometimes the pools do completely dry, with the result that fishes such as *Aequidens* expire along with others not able to respire atmospheric oxygen, move overland, or find protection by some such specialized means. Up to a certain point of concentration it is clearly valuable to the survivors to have their numbers reduced, which function *Aequidens* performs with much vigor. However, it is also evident that if the evaporation proceeds at a pace with which the killing off cannot keep up, the amount and number of dead fishes would only serve to hasten the death of all by their polluting effect. It might be thought that conditions as above are unlikely, and that the killing of excess fishes could always far outstrip desiccation. Such is not the case because the fights staged by *Aequidens* are not rapid affairs but usually take several days, even in an aquarium, to come to a fatal climax. Then, too, evaporation in the neo-tropical regions is not infrequently rapid, both from the surface and by soaking into the thirsty soil.

¹ These three forms have also been observed in the New York Aquarium where they will fight excessively if present beyond some critical concentration. See Breder and Coates (1933) for details regarding *Pomacentrus*.

Breder and Coates (1932) showed that in *Lebistes* the eating of newly born young is a direct coefficient of crowding. This fish, which may be thought of, relatively, as producing a continual stream of offspring, living in a large school can well cope with the population problem in this manner. *Aequidens*, on the other hand, producing comparatively occasional broods and not in schools, and protecting the young fish by means of an elaborate behavior, cannot control population by simple, direct infanticide but has recourse to adult destruction as previously outlined. Stating it another way these two reproductively different species differ in their solution of the population problem in accordance with their methods of procreation; *Lebistes* under crowding, simply eating the young as fast as they are born, and *Aequidens* fighting to kill off too near neighbors and then resting as a group, when such would be fatal, awaiting their doom or release according to the fortunes of weather.

The physiological cause of this reverse in the attitude of *Aequidens* towards their companions has become clear as a result of analyzing the conditions under which they do and do not fight. Below a temperature of 22° C. fighting becomes less frequent, and at 20° C. stops altogether. Between a range of pH 6.0 to 7.3 there seems to be no clear relationship to that measure except so far as the amount of free carbon dioxide modifies it. When the concentration of CO₂ is less than about 0.90 mM fighting generally occurs. When above that it generally ceases and at 2.00 mM it stops altogether, but suffocation does not commence to evidence itself before over 3.00 mM is reached. While the exactness of the measure cannot be pressed too far because of the difficulty of determining the actual "end point" of such a reaction as "fighting," it may be noted that at a temperature of 26° fighting stopped at 0.42 mM CO₂, whereas at a temperature of 21.5° it continued at a concentration of 0.82 mM CO₂. Typical readings are given in Table I. Since low temperatures are not involved in dry season pools, it follows that the CO₂ concentration determines the interesting change of attitude under crowding that may have a distinct survival value in a state of nature.

In addition to taking some locality for their own, usually a corner of an aquarium, *Aequidens* goes to some trouble in modi-

fyng it to suit. A hole is generally excavated in the sand, or if that is covered with a sufficiently thick layer of detritus the latter only is removed. This has generally been considered only as part of the breeding behavior, in aquarium literature, and although the matter of hole digging does appear again in that connection, the following evidence demonstrates that the excavation of holes is primarily associated with the establishment of a retreat and is not an integral part of the reproductive habits.

Four compartments were arranged, as indicated in Fig. 1, to provide for four male fishes. A detailed consideration of this illustration and its explanatory legend shows distinctly that these fishes usually dig excavations in the most protected parts of the aquarium. After fifteen days of being left alone, with only nominal disturbance, all four fish excavated holes along the back and two along the front as well (Fig. 1-1). On smoothing out the sand, two dug where they had before, and one in a new place, although one had the choice of a ready-made hole (Fig. 1-2). Again on smoothing the sand and protecting the sides all around, each fish accepted the "artificial" retreat, although only one was in the original place (Fig. 1-3). On removing the cover one, fish A, went back to its original location (Fig. 1-4). A female was next placed with the male B. No further nest building occurred there but C, which could see these two fish, dug a hole farthest from them diagonal to their nest. Females also dig holes. This one, removed to a circular jar, dug in the center. A dark card and a light one were placed on either side of the tank. Then a hole was dug nearest the dark card. An introduced male induced no further excavation. This experiment was used as a check on numerous observations and establishes that *Aequidens* of both sexes digs retreats adjacent to dark surfaces and that these lack association with reproductive activity, since some of the fishes were not in breeding condition. Further, there is a strong tendency to return to the same spot for building a retreat if a conditioning has once been established and if there is none, such as in the case of a fish newly placed in an aquarium, there is a general acceptance of existing retreats even if they are not in what might be considered the most acceptable position. Dissatisfaction with an aquarium appears to stimulate continual

digging as a response to much disturbance, such as too great activity in sight of the fishes, especially if the aquarium is very small. In one such case, in a small exhibition tank of the New York Aquarium, the fish in question moved all of the sand from one back corner so that he could scarcely be seen. Further work would eventually cut the excavation through to the front glass. When this happened he would begin all over at the opposite end and repeat. This went on as a daily performance until the fish was moved to more commodious quarters.

MATING

The details of sex recognition may not be altogether evident but would seem to be peculiarly simple. As the reproductive urge begins to make itself felt the males, at least, become more active and make forays farther and farther from their retreat, accompanied by an ever brightening of the coloration. Sexual dimorphism is not great in this species. Aside from somewhat longer anal and dorsal filaments and slightly more brilliant colors, there is little to distinguish the sexes. Even to this there are exceptions, so that not infrequently a fish taken to be of one sex, by comparison with its tank mates, sometimes turns out to actually be the other. Unless there is some chemical differentiation that we cannot readily determine, it is doubtful if sex is really distinguished by ordinary sensory perception. It would seem that the reaction between any two fishes is identical, subsequent behavior leading to fighting ordinarily, or to reproduction if both specimens are properly sexed and physiologically ready for spawning. When two fishes approach they normally line up for fighting purposes. This may be head-on with mouths open, or side by side, head to tail, when a peculiar rocking motion on the part of one or both is indulged in. Such activity usually results in torn fins of the smaller of the two. This is true of two males, or a male and a non-breeding female. Two females have not been seen to maul one another in this manner.

All or part of the above also takes place even when spawning is subsequent so that the female or sometimes the male, or both, may spawn with the fins torn. It seems that when a female is

ready to spawn she does not retreat as far, or at least is not completely routed. As spawning becomes more imminent the side to side position is assumed with increasing frequency and less actual fighting takes place. Finally there comes a time when the female in such a position gives a peculiar quiver to her dorsal and anal fins, which is not easily described in detail. This seems to be a signal of impending spawning and fighting rarely occurs after it. An item for which no explanation is offered is that after spawning has once occurred the pair seldom fight again, but generally live in peace spawning repeatedly thereafter. The fish never leave one another for any great distance, and much time is spent apparently searching for a place to deposit the eggs. This is usually a rock that is cleaned by fanning away any detritus that may be present, and picking off any larger object with the mouth. In an aquarium, in lieu of a suitable rock, the glass walls may be used although an opaque surface is preferred. Experimentally, a glass painted black on the reverse side will be selected in preference to a transparent piece. If there is only a thin layer of sand a spot may be cleared free of this cover but holes are not dug for this purpose. A considerable variety of surfaces were presented at one time or another which resulted in the conclusion that a large variety of factors enter into the choice of a site. A dark rock will be selected in preference to a light one, but any rock will be picked in preference to any glass. This may have to do with the texture of the surface. A rectangular cement "box" with a partition near one end was constructed to give a variety of surfaces. The first spawning was on top, as shown in Figs. 7A, 9A and B and 10A. The second spawning was on the side as shown in Fig. 7B. It is to be noted, however, that the vertical surface was selected only after the block had been moved so that there was more swimming room between it and the glass side. There was no disposition at any time to spawn under the shelter of the construction. At one end there was a shallow shelter and at the other a deep one. The fishes, sometimes, when not breeding hid just within the entrance, but never went out of sight. The site of the egg deposition may or may not be near one of the earlier made holes, but in an average small aquarium there is little opportunity to recede very far from it.

The actual deposition of spawn may be studied at close range as the fishes are usually so intent on the process they are not readily disturbed. Apparently, spawning is usually or probably always done in daylight. *Aequidens* is quite inactive at night, both in the natural state and in aquaria. Since it was already known that under the conditions in the experimental aquaria spawning occurred about every twenty-five days, it was a simple matter to plan long in advance for the anticipated egg laying. The aquarium was arranged in such a fashion as to cause reproduction to take place in a readily visible location. As the choice of egg laying sites was already well understood, the tank arrangement became a simple matter and the only requirement was to be on hand at the prognosticated time. The details of one spawning studied intently, which included the use of a hand lens, may be considered as typical.

Spawning commenced at about 10.00 a.m. and was not completed until about 12.30. The eggs were laid on a rounded cement disc especially made for such a purpose. Just prior to depositing the first eggs the female engaged herself in a final "cleaning" of the spawning site by continually biting at the rock. At the same time a more or less violent quivering is observable. The male takes no part in this final procedure, merely swimming about leisurely close to the rock. At this time the ovipositor of the female and the inseminating tube of the male are both extended to their full limit. The former is decidedly blunt and larger in diameter than the latter which is pointed. See Fig. 2-A and B. Both point slightly backward. According to C. W. Coates (personal communication) those of *Cichlasoma nigrofasciata* Günther, point slightly forward as do those of the pomacentrid, *Pomacentrus leucoris*, Breder and Coates (1933). The female proceeds to drag the ovipositor gently over the rock surface with the tips of the long ventral fins trailing out on either side. The eggs come singly and may be seen passing down the translucent tube. The fish comes to rest generally when the egg is about half extruded. Due to the fact that the tube is bent backward because of being dragged over the rock the eggs are held free of it until the female slows her motion a little, or rises slightly so that the egg comes in contact with the rock surface.

Here it adheres and the female passes on to repeat the process. Usually the tube crumples slightly and were it not for its flaccid condition would appear to be used to press the egg in place. This is certainly not the case as any significant pressure would be mechanically impossible by such a feeble structure. As the female pulls away from the egg a slight quivering of the body may be noted. A diagram of the action of the egg laying is given in Fig. 2—C, D and E. The above description gives the simplest of the behavior in egg laying. About half of the time the ventral fins assist in expressing the egg. It would seem that the passage is not always entirely easy. Under such conditions the fins are brought together, slightly pinching the tube between them and are then pressed downwards, resulting in stripping the tube of the egg. This action of the fins is naturally very gentle and weak, due to the poor leverage, but is apparently adequate. In addition to the mechanical side of the performance, there may of course be some nervous stimulation that is not so obvious.

The male is in no way attentive to the female proper but proceeds to drag his inseminating tube over the rocks and eggs in a similar manner to that of the female, stopping and quivering every so often. Apparently at such times the sperm is ejected, but in such small quantities that nothing could be seen that for certainty could be designated a cloud of sperm. The male does not usually follow the female about but moves over the eggs, rather independent of her, trailing his fertilizing tube over the eggs generally where she has been recently depositing spawn. Although he is as likely as not to be at right angles to her on encountering new eggs, he is apt to line up where she was while the fluid is emitted, as evidenced by the characteristic tremor. By this time the female has usually moved on and is headed in some other direction. It would seem that the presence of the new egg stimulates the male to emission. Possibly the greater adhesive quality of the newest egg or eggs has a stimulating effect that is lost as soon as they water harden. In any event he goes over the entire patch so often that it is unlikely that any would be missed, even on a most haphazard fertilization. The actual spawning is illustrated in Figs. 5 and 6A. The latter shows the

fish in as close an approach as they ever make to each other. The male is on the left following the female.

The first eggs are laid in rather rapid order and may be along straight or slightly curved lines to the number of five or six. This explains the presence of such groups that may be seen in each photograph of the eggs in this paper (especially Fig. 8). Beldt (1923), one of the relatively recent writers in small aquaria journals, states that about twenty eggs are laid in a row and that the male fertilizes them as soon as a row is laid. The writer observed no rows as long as that, nor that the male paid any particular attention to rows, as such. With longer rows, however, such behavior might become apparent. After several such groups have been laid the female passes over and over the cluster, placing an egg wherever there is room, which explains the presence of those not in lines. The spacing of the eggs is likewise evident, the minimum being accounted for by the thickness of the walls of the ovipositor. After a fair number of eggs have been laid, the remainder seem to be under less pressure and the actions are more deliberate. At such times the female may be seen trying to fit the ovipositor with its contained egg between two previously laid. Near the end of spawning the eggs come with much less frequency, but also the available spaces between previously laid eggs become fewer, resulting in longer and longer periods of "feeling" for a vacancy. Frequently, at such times, the female apparently unable to retain the egg any longer, rushes to the edge of the cluster and makes deposition well beyond the main group. This clearly accounts for the scattering or thinning of the eggs toward the edge of a group of spawn. This feature is likewise indicated in each of the photographs. Thus it becomes evident that the characteristic pattern of the egg cluster of *Aequidens* is explainable on a purely mechanical basis in which the scattered lines of eggs, the irregularly placed ones and the thinning toward the edge of the group are all functions of (1) the speed with which the eggs are delivered, and (2) the tendency to lay the eggs as closely together as the size of the ovipositor will allow.

On the completion of spawning, the male moves off to stand guard and the female fans the eggs. The genital tubes shrink

to a small size within a half hour and the characteristic defense behavior against intrusion takes place. The male in Figure 10A of another pair, still plainly shows his shrinking genital tube. Spawning may take place at a temperature of about 26° C. but one pair in running tap water spawned at 21° C. Beldt (1923) found them breeding at 70° F. and that they could withstand temperatures as low as 56° F. Breder (1927) found the Panama fish breeding between 76° and 86° F. The color of the eggs in all cases was a deep amber but Beldt (1923) describes the color as red. If this is not an error, there is more variation in this regard than would be supposed from the writer's experience. All other mention of egg color in the aquarium literature agrees with the author's observation. The number of eggs deposited at one spawning as indicated in Table II ranges up to 485 at least. Beldt (1923) gives a range of from 200 to 350 and the time of laying as forty-five minutes which is considerably shorter than the observation described herewith which, however, is in accord with the fewer eggs. As indicated in Table II the eggs, under our conditions, hatch in two or three days. Beldt (1923) gives four days.

PARENTAL CARE

The most striking features in the reproduction of *Aequidens* are involved in the details of parental care. The parent fishes cooperate to a remarkable degree in this feature of behavior. As soon as the eggs are deposited, which event may occupy several hours, both parents occupy themselves by circulating the water over them, as noted by Beldt (1923). This may be done by the pectoral fins, or by waving the caudal as well as the long lobe of the anal fin. Usually only one fish at a time thus works over the eggs. The other cruises about nearby as though scouting for possible enemies. If the eggs are more spread out than is generally the case both parents, at times, may work over the eggs simultaneously. Such behavior is shown in Fig. 9A. After a period varying from one to fifteen minutes, the guarding parent will approach the incubating parent and then they will change places. This changing of the guard is illustrated in Figure 6B which shows the female coming to relieve the male. The guard-

ing parent alone takes "time out" to feed. The taking of food is almost always followed by a quicker than usual return to the eggs, a reaction tending to insure that both get food? Coates (1932) describing the behavior of the parents of these fishes, in a tank containing various species, states it as follows. "At feeding time the male would dash into the milling swarm of fishes congregated about the falling food, snatch a few mouthfuls—always keeping a wary eye on the manoeuvring of the other fishes, ready to drive away any that appeared unduly interested in his nest—and then swim over to the nest to relieve the female of her nursery duties. Immediately upon his arrival, but not an instant before, she would hurry over to the feeding place and, while snapping up some food, ably perform the policing duties of her consort. After a few mouthfuls she would return to the nest, and the male would come back for more food. This interchange of duties would occur as many as three times before the hunger of either was appeased." Scores of observations show that the male spends more time fanning the eggs than the female.

It has been generally assumed that the above described behavior has to do with an adequate aeration of the eggs. That this has nothing to do with such activity, on the part of these fishes at least, is established by the fact that they will hatch just as well when removed from the parental influence. This is directly contradictory to Beldt (1923) who states, "Were you to remove the parents as soon as the eggs are laid they would decay." Figure 8D shows the newly hatched eggs of Figs. 6B and 8B, which had been taken from their parents. Although in an aquarium this behavior is thus patently unnecessary to the hatching of the eggs, in a state of nature it undoubtedly is of genuine significance on two counts at least. Small, exploring, bottom life destructive to fish eggs, such as crustacea and worms, may be certainly kept off by such means, while the guarding parent fends off larger attacks, such as other fishes. Both these effects have been observed in aquaria in which such organisms have been placed or kept. Coates (1932) writes as follows concerning defense of the nest: "At no time was the nest unguarded, and likewise at no time were the other inhabitants of the tank free

to go where they pleased. They were all herded into the end of the tank farthest from the nest; unmolested if they did not wander, but unceremoniously hustled back if they did." Chute (1933) states "... it is a common sight at the Aquarium to see, in a tank holding ten or fifteen *Acaras*, two pairs of fishes fanning eggs and a third pair guarding a flock of young fry, while they take turns herding the unoccupied adults into one corner of the tank." Possibly even more important is the prevention of suffocation of the eggs by the silting processes of most natural streams. In the Panama waters inhabited by *Aequidens coeruleopunctatus* such silting is general and fills all small depressions. On the other hand, the nandid, *Monocirrhus polyacanthus* Heckel, which hangs its eggs on the underside of a leaf, Coates (1933), where they are automatically protected from silt, shows not nearly as much current producing activity, acting more as a standing guard. While its vibratory fin tips produce a fair current, this movement is normal in the resting fish, just as it is to *Umbra*, Breder (1925).

At times when *Aequidens* are not caring for eggs or young they flee from any object intruded into the aquarium. When eggs are present the fish are very aggressive and will attack fingers or net, at times holding on with their minute teeth and shaking bulldog fashion. A small rock quietly introduced shares the same fate. One fish was observed to "work" on such an object for nearly an hour. Removal of the eggs causes the fish to lurk in the vicinity for some days. Both parents attacking an intruding hand is shown in Fig. 9B. The male, to the left, is half turned in his effort to tear out a piece of flesh.

The question as to what stimulus causes this response naturally arises, for non-breeding individuals will attack and eat either eggs or young of another pair. This seems to be one of the chief problems of a pair in tank containing other fishes, either additional *Aequidens* or different species. The greater aggressiveness of the parents seems to "bluff" even specimens much larger and there is usually a short chase only. At no time has such a raider been seen to offer fight. Aside from physiological changes incident to spawning, what may account for the observed behavior? Are the fish attracted to the eggs or to the site at which

they spawned? In order to determine this the following experiment was undertaken. Two identical cement blocks were prepared and placed in an aquarium with a pair of fish about ready to spawn. Realizing the preference of these fish for a rock, rather than the glass walls of an aquarium, it was anticipated that they would spawn on one of them. This occurred in due course of time. This was a second spawning on such a block similar to that shown in Figs. 5 and 6A. The following day a dark glass was dropped into the aquarium and the two fishes herded behind it. Then the two cement blocks, one holding the eggs and the other not, were quickly reversed as to position, as shown in Fig. 3A. It was expected that the fish would either tend the eggs in this new position, or stay at the old site. When the opaque partition was removed neither happened. For some time the parent fish took no apparent notice of either block but cruised about the tank as do fish that have been recently netted. In about an hour they were seen picking the eggs off the rock. These were then stowed in the bottom of an old excavation farthest from the front glass. Here they were incubated after the fashion of centrarchids. It is thus evident that the place of oviposition does not determine the parental behavior. Further than this it demonstrates that these fish are sufficiently responsive to environmental modifications to resent such changes by decamping with their family to a new site. So far as the writer knows, this has no parallel in vertebrates lower than mammals (*e.g.* the domestic cat) and has none in the egg-laying vertebrates. It is stated in the popular aquarium literature that various related cichlids may lay their eggs either attached to a solid support or in a sand depression. On a basis of the above it would seem likely that the cases of laying eggs in the sand may only be cases of such change of locality due to disturbance, and described from fragmentary observation.

On toward the time of hatching, the guarding parent becomes more and more industrious in digging new holes. While the difference is slight it would seem that the female is the more active in this regard. This may be simply because the male does the bulk of the egg fanning. The sand digging operation is well illustrated by Fig. 10B. The force with which the sand is ejected may be noted by the distance of the particles from the

fish as they fall down the glass wall. Shortly after the eggs have hatched they are removed by the parents to one of these newly made depressions, usually one larva at a time, as was also noted by Beldt (1923). They are gently picked off from the shells to which they hang by their adhesive organs. Eggs that are dead are likewise picked off but whether or not they are segregated could not be determined. The young fish are usually placed in one depression but may occupy two or even three. It would seem that the "team-work" of the parents is not perfect at this point, one favoring one hole and the other another. From now on until the yolk sac is absorbed and the young fish rise from the sand in a cloud, the parents' efforts are mostly those of guarding. Occasionally they will take up a mouthful of young fish and blow them back in the nest which seems to serve to prevent their packing into a suffocating mass, or, more likely, has to do with the problem of silting in a state of nature as already alluded to. The young without parents suffer no inconvenience in an aquarium but scatter out widely. The method of handling is entirely by sucking in on the respiratory current and ejecting by the special method fishes use in blowing out water, as described by Breder (1925a and b).

After the fish have risen, about three days later,¹ the parents' activities are of three distinct parts. There are always stragglers lagging behind the school of young fish, or precocious ones darting ahead or to one side. These are picked up and blown back into the mass with considerable violence. A male gathering up venturesome offspring to return them to the nest, is shown in Fig. 11A. Guarding the young becomes more difficult but is carried on with equal energy. Hole digging seems to be of a specialized kind. It is persisted in but the holes are small and shallow. As soon as a small hole is dug, accompanied by a flurry of fine debris, the young swarm into it and apparently feed on the small particles brought up. As the young grow the relationship with their parents becomes progressively more loose. At about twenty-five days from the egg laying, the parents are generally ready to spawn again, at which time they usually lose all interest in their earlier young, and may eat them if not

¹ See Table II. Beldt (1923) also gives this figure.

too well fed. The few that do escape merge with the next brood when the latter rise from the sand but are readily distinguished by their much larger size. If the eggs are removed, as previously described, and the young returned to the parents when able to swim, they are devoured as any food object. The parental instinct is thus destroyed by absence from the eggs. On the other hand, young from another brood are not distinguished by the parents from their own, even if of a considerably different size. In fact one pair attempted to herd two young *Lebistes reticulatus* together with their offspring. The efforts of the *Lebistes* were those of violent escape, quite different than those of the young *Aequidens*.

REACTIONS OF THE YOUNG

The preceding description of the attitude of the parents toward the young presents a very inadequate picture of the family life of *Aequidens*, since it is an integration of such factors with those of the young fish themselves. The tropisms of the young fish give valuable clues to the complicated reproductive activities of the species since they are not overlaid by the various conditionings that help to becloud the elements involved in the parents' behavior.

The newly swimming larval *Aequidens* are negatively heliotropic in a rather weak fashion. In a simple aquarium without fittings they will regularly gravitate to the darkest end. They will not, however, go into a completely darkened portion but may possibly be better described as seeking some optimum of light intensity. This is apparently similar to the behavior of young toads as described by Riley (1913). Young reared in the presence of the "breeding block" shown in Figs. 7, 9 and 10 never entered its shelter although they sometimes stayed within its shadow, nor did the parents try to urge them to it but dug new holes for them as shown in Fig. 10B. The visual stimuli appear to be by far the most predominant ones. Cutting across the negative heliotropism, and sometimes directly opposed to it, is a positive response to moving objects. This is not interfered with, either by size, color, degree or kind of motion, through a

wide range. It is this that certainly keeps the school of young fish together, and in company with their parents. The limiting factors of reaction are purely mechanical, such as distance of moving objects in relation to size, intensity of light, amplitude and speed of motion.

In the experiments used to define these responses, flat cards of the sizes shown in Figure 3B were employed. These were suspended from a pivot so that they could be swung to and fro at a distance by means of a cord passed over a series of pulleys. Figure 12 shows the position of a school before and after moving a dark oval card. In this case the moving target was suspended in a beaker within the aquarium, but it worked just as well entirely free and outside of the tank. Figure 12A shows the fishes in a school at the dark end of the aquarium, taking no heed of the target about the size of their parents, and Figure 12B shows them clustered about it a few moments after it had been slightly oscillated, contrary to the negative heliotropism. At a distance of 30 cm. object number 1, in Figure 3B, caused an appropriate reaction, as did a black and a white card 3" x 5" at a slightly greater distance. Items 2 and 3 of the same figure would induce a reaction at a closer distance only, and item 4, which was merely the bare wire that supported the cards, would work not farther away than 5 cm. A further complicating reaction is that any sudden change to either a brighter or duller light intensity causes the fish to drop to the bottom. Tapping on the glass, as when in Figure 12 the target is oscillated too far, had no apparent effect; but a violent agitation, such as a very heavy jar to the table, would cause them to drop to the bottom.

These reactions together with those of the parents may account for the entire behavior ordinarily observed which sometimes appears to be very complicated. In a wild state the value of these reactions is quite apparent. The negative heliotropism to strong light tends to keep the fish on the bottom, as all the bright light under such conditions comes from above, while the positive heliotropism to weak light keeps the young fish out of dark holes that may hide lurking predators. The positive reaction to moving objects of any size keeps the schools together and in company of the parents. The dropping to the bottom on a sud-

den change in light intensity keeps the fish where they are best able to be protected by the parents when a larger fish passes overhead, or an overhanging plant is brushed aside by some stream-side animal. A slight mechanical jar would not likely occur in their native waters, but to a violent action, such as the planting of a hoof in the water, they are negative. One of the characteristic acts of the parent fish with young at this stage, when danger threatens, is to immediately swim over the school of young fish and snap the ventrals out fanwise. This may be repeated several times before he dashes to attack the intruder. The young fish consequently drop to the bottom. It is little wonder that such behavior has led the uncritical to write in an extreme anthropomorphic vein about cichlids, vesting them with all manner of human attributes.

As the fishes grow larger and sturdier these reactions become gradually less and less pronounced. At one point, when the young are about six days old, the small school takes on characteristic "streaming" movements. Not infrequently these form a figure eight as indicated in Figure 3C. The young in this aquarium passed through this double loop in an average time of 12 seconds, showing them to have a speed of about 5 feet per minute. This is naturally before the time they scatter out and its function, if any, is not clear. It is imperative that the young leave the parents before another spawning, however, which may be as soon as twenty-five days. If this does not take place the old fish try to guard the young indefinitely and very likely accounts for some fish seen in Panama with exceedingly large young. After they once leave the parents, the cycle is completed, with the young going on to maturity. Certain other items of behavior, not readily discussed with the foregoing, have been relegated to the following section. Some are explainable at this time and others are not, but in some ways they form the most interesting items in this study.

EXCEPTIONAL ITEMS OF BEHAVIOR

In the case where eggs were deposited on the black partition of aquarium "B" of Fig. 1 and shown in Fig. 8C, a most

remarkable performance took place in aquarium "A" which still contained the solitary male originally placed there for the hole-digging experiments. This fish took up a position on its side of the perfectly opaque partition and proceeded to fan and otherwise father the area exactly opposite, the spot covered by the eggs. Fig. 13A shows the two fish on either side of the glass in characteristic poses.¹ It was first thought that the possible chemical emanations from the eggs, passing through the slight crack between the partition and the aquarium side, attracted this male fish. That this was not the case became evident later as this fish carried on his incubating efforts for the entire time, stopping only when the parents had removed the young to one of their sand pits. The exactitude with which this fish covered the area corresponding to that occupied by the eggs, can still not be adequately explained at this writing. As vision and chemical sense could not well account for this effect, sound and mechanical jar were considered; especially the latter as the fishes on either side of the partition actually attempted to fight through this opaque wall through which they could not possibly see their opponent. In various places they would bump their noses against the glass exactly opposite to each other. These fighting regions were generally somewhere near the eggs, but sometimes as much as half way across the tank. Observation of such behavior lead to an experiment based on a modification of the targets earlier described in studying the tropisms of the young. The oscillating member was set up, as shown in Figure 13B. A piece of rubber tubing was placed on the moving end at an angle so that it could be made to tap the partition on the egg-bearing side with any degree of firmness. Light taps such as the fish might give caused no response, and stronger ones merely induced the fleeing reaction which was only temporary because of the strong attraction to the place opposite the eggs. Further observation revealed the real cause of the "fighting through the wall" which proved to be as simple as it was mystifying.

The crack between the glass side of the tank and the black

¹ It will be noted that the excavations in the sand in this and the following three pictures do not tally exactly with those of Fig. 1-5. This is because these photographs were taken much later when still other holes had been dug. Close inspection will, however, show the original excavations of the earlier period.

partition was not more than one-eighth of an inch wide. Due to the large angle of vision of these fishes they could actually see each other through it. This was checked by placing smaller strips of black glass against the aquarium walls but sufficiently distant from the partition not to interfere with a free interchange of water so as not to inhibit any chemical effusions. Under such conditions all fighting stopped only to reappear again when the baffles were removed. This completely explained the fighting at the edge of the partition but not that remote from its edge. Long and continued observation explained this also as it was noted that all "fights" started at the crack. In their struggles to get through at each other, each fish struck the aquarium wall and then moved back from it (or knocked itself back). Then they would be facing just about opposite each other and if first noticed in such a position were decidedly puzzling. It may well be also, that the tapping on the glass of the opposite fish influenced them to continue even if mechanical imitation could not initiate such behavior.

Before attempting to explain the attitude of the lone fish, toward the eggs, the events following hatching may be mentioned. At the time the young began to rise and swim around, some young fish of another pair were introduced to both aquarium "A" and "B." Those in "B" were absorbed in the "family" school and the male in "A" immediately took characteristic parental care of his charges. This is entirely unlike the behavior of non-breeding adults which see the little fish only as food objects. This is even true when some are returned to parents whose nest has been robbed as has already been pointed out. Further than this, as the young fish grew and became more adventuresome, the male in "A" managed to rob the true parents. He would lie in wait near the crack and as a young fish came close literally suck it through the crack. Fig. 14A shows the two aquaria with the young fish up and active. The fish in "A" has just begun to gather the school together. Fig. 14B shows a later condition where he had actually rounded up the bulk of them on his side of the wall. From then on much of the time was spent with the fishes on either side of the fence taking the young fish back and forth (Fig. 14C). Sometimes most were on one side and some-

times on the other. This was kept up until the fish were removed to make way for other experiments.

An attempted explanation of the unusual behavior of this solitary male is offered for whatever it may be worth. Since these fish normally eat the young of others unless they are tending a brood of their own, and since the male in question showed all the reactions of a fish that had just spawned, it is supposed that while the pair in "B" were spawning on the glass partition, the male in "A" became stimulated to discharge its gonads, directing attention to the crack through which the female could be intermittently seen. In fact it is not impossible that some of the eggs may have been fertilized by the extraneous male. Of course if the partition had not been there, one male or the other would have been vanquished and probably killed.

In a large aquarium containing a stable population, not unlike that described for *Lebistes* by Breder and Coates (1932), it was not uncommon for as many as three pairs to be caring for young at the same time.¹ Apparently these broods would never get mixed up. Observation showed that they closely approached, but would veer off from each other just as they would be about to merge. Since the schools were always composed of slightly different sized fishes, they could be distinguished. That the size difference had no bearing on it is shown by the merging of the remnants of an earlier school with a later as previously described. Incidentally, the schools in this larger tank were always more compact due to the greater attention given by the parents presumably because of the aggression of non-breeding fish. Eventually, most of the young would nevertheless disappear that way, just enough growing up to replace deaths from other causes.

DISCUSSION

The study of the reproductive habits of *Aequidens latifrons* makes clear the fact that these fishes excavate holes for both the purpose of modifying their environment to suit their convenience, and also at the time of breeding as receptacles for their young. It has also been shown that to a very remarkable degree

¹ Chute (1933) made similar observations in the much larger exhibition tanks of the Shedd Aquarium in Chicago.

these fishes will modify their behavior to suit a given set of circumstances, as for example the case where a pair removed their eggs from a rock, following disturbance, and incubated them in a sand hole not unlike the method of the centrarchids. Given such a tendency to transport both eggs and young under appropriate stimuli, it is not difficult to imagine how oral incubation may have arisen. Continual annoyance in a state of nature by other creatures may have induced continued transportation until finally no resting place at all was selected, Breder (1933).

Checking from the other end, that is, from species that carry their eggs regularly, there are other evidences to support this view. While these experiments were in progress a pair of *Tilapia heudeloti* Dumeril, were also studied. While the full details of their reproductive habits will not be gone into at this time, the following remarks are distinctly pertinent. Prior to spawning, a large but shallow hole was dug, approximately in the center of the tank, and all loose detritus brushed back. The eggs were deposited in the hole and immediately gathered up by the male. As there is an obvious necessity for depositing eggs in a place from which they may be recovered, the retention of hole digging and cleaning as a habit is clearly of survival value. Another species, *Haplochromis strigigena* Pfeffer, that carries its eggs about, may or may not prepare an excavation for the eggs, as is well known. Whether or not a nest is made seems to depend on the aquarium. If large, and with a quantity of detritus on the bottom, a nest is likely; whereas in a scrupulously clean, small tank, one is unlikely. Here, again, seems to be a well-marked disposition to fit the behavior to the condition. In this species the females normally take care of the eggs, but as Breder (1918) has shown, the male may sometimes take on the role. As one fish normally takes care of the eggs, the tendency for either or alternate sexes to take the role would seem to be relict of a time when both were interested in protecting the young. The fact that the brooding type normally alternate their attention to the eggs, further suggests a reason why both fish do not each take some. Actually, this does occur in the oral incubating *Betta pugnax* Cantor, which derives its habits from a different basic type. A further consideration of the significance of these differences will

be discussed in a later communication. Apparently, the origin of oral incubation in the Siluridæ, on the other hand, had its inception in a habit closely similar to that of the Cichlidae. As pointed out by Breder (1932), incubating *Ameiurus* frequently take their eggs in their mouth and churn them about. This, which has a special significance, will be discussed in full in a detailed consideration of their reproductive habits.

SUMMARY

1. *Aequidens latifrons* may lay eggs as frequently as every twenty-five days at a temperature of about 25° C.
2. The eggs are fanned for the full period of incubation and the young protected until the parents are ready to reproduce again.
3. The adhesive eggs are attached to a solid support, preferably an opaque one, such as a rock, up to the number of about 485 at least.
4. If the fish are sufficiently disturbed the eggs may be removed, carried to some hollow in the sand, and incubated there. This behavior suggests the inception of the buccal incubation of other genera of cichlids. Further disturbance will sometimes result in the young or eggs being eaten.
5. Holes are regularly excavated in the substrate and act as lurking places, and, at times of reproduction, as sites to place the newly hatched fish before they are able to swim, or for the eggs if the original site is disturbed.
6. The young are negatively heliotropic, move toward any moving object of sufficient size to be detected, and descend to the bottom on any sudden change in light intensity to either greater or lesser brilliance and to violent mechanical jars. These reactions, coupled with those of the parents, account for most of the apparent, complicated, family relationships.

7. Sex recognition is accomplished by the differential behavior of a female ready to spawn as compared with that of males or non-spawning females which fight on approach.
8. Well established areas of proprietorship are patrolled by *Aequidens*, usually about some natural retreat or sand hole. Neutral areas exist where fighting does not ensue.
9. Artificial holes are sometimes accepted, chiefly in strange aquaria where there has been no conditioning to previous places. Under the latter conditions a hole may be re-dug repeatedly in one spot after having been destroyed.
10. Hole digging may be intensified by continued annoyance and confinement in too small a container.
11. Fighting is somewhat a coefficient of crowding up to a certain point of concentration beyond which it falls off, due apparently to the establishment of an unnatural condition or one simulating the excessive crowding witnessed in the dry season of the native streams. The value of this reversal of habit is evident when it is considered that the resulting dead tissue from excessive deaths by fighting would reduce the chances of survival of the remainder by pollution. The increase in CO₂ concentration acts to inhibit fighting as here noted, but long before the suffocation threshold is reached.

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¹ Since this study went to press, Dr. G. S. Myers presented a paper at the Seventeenth Annual Meeting of the American Society of Ichthyologists and Herpetologists entitled, "A Possible Method of Evolution of Oral Brooding Habits in Cichlid Fishes." The views expressed therein are in essential agreement with the present concerning the origin of oral incubation, and with the abstract of Breder (1933). It is noteworthy that these two workers independently find their conclusions in such full accord.

TABLE I

Fighting Reactions of *Aequidens* under Varying Conditions

Attitude	mM Free CO ₂	mM Combined CO ₂	pH	° C.	Date
F	0.25	2.24	7.3	26	June 13
N	0.42	2.96	7.3	26	13
F	0.29	1.69	6.8	23	14
N	2.01	1.88	6.1	26	14
N ¹	3.15	1.69	6.0	26	14
F	0.82	1.96	6.6	21.5	15
N	7.0	20	16
F ²	7.0	21	19
N	7.0	20	20
F	7.0	22	24
N	7.0	22	25
F	7.0	22	27
F	0.37	0.27	6.8	22.5	July 11

F=Fight. N=No fight.

CO₂ readings made with a Van Slyke apparatus; pH readings made with a LaMotte comparator, both by T. H. Howley.

¹ Fish suffocating.

² Fighting slight.

TABLE II

Reproduction Data on *Aequidens latifrons*

Spawn No.	Pair of Fish	Spawned	Hatched	Arose from Nest	Days since Spawning	No. of eggs	Temp. ° C.	Eggs placed on	See Fig. No.
1	A	May 5	May 6	May 11	..	485	25.5	white rock	6B, 8B, D
2	B	May 5	May 8	May 11	..	358	25.5	black glass	8C, 13, 14
3	B	May 30	June 5	25	round block	3A, 5, 6A
4	B	June 24	June 27	25	486	26.	round block	2, 8A
5	C ¹	June 28	21.	slate bottom
6	D ²	July 15	23.5	round block
7	B	July 17	July 19	23	300±	23.5	top of square	7A, 9, 10
8	E ³	July 31	Aug. 2				side of square	7B

¹ In running tap water.

² Same male but different female from pair "C."

³ Female from pair "B"; male from pair "D."

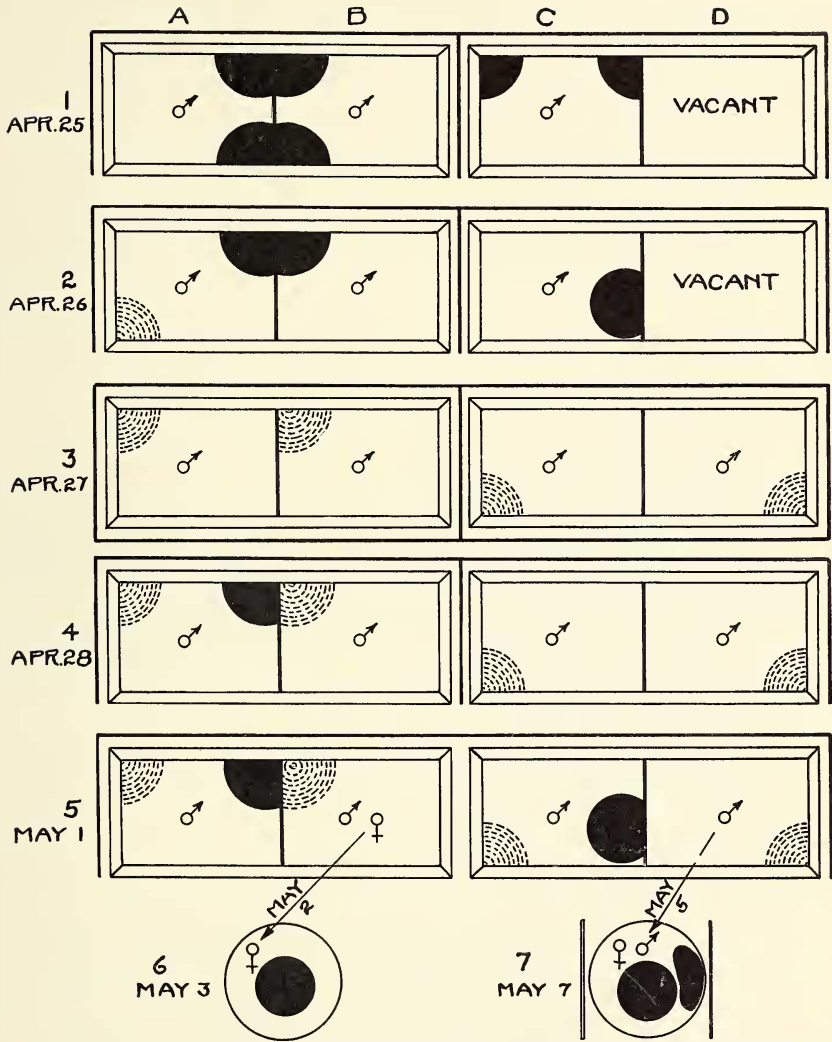


Fig. 1.—The excavating habits of *Aequidens*. A, B, C and D represent two aquaria, each bisected by a black glass partition. The outer black lines represent cardboard walls further restricting vision outside their aquaria. Black areas represent excavations made by the fishes. Dotted areas represent excavations made by hand in imitation of the retreats. Sex symbols indicate number and sex of specimens. See text for explanation. 1. Condition of aquaria after standing for fifteen days. 2. Condition of aquaria after smoothing of sand the day previous, and the construction of an artificial retreat in "A". 3. Condition of aquaria after smoothing the day previous, and the construction of an artificial retreat in each aquarium, coupled with a complete blinding of each aquarium. (Note especially the board walls.) 4. Condition of aquaria after the removal of the front wall. 5. Condition of aquaria three days after introduction of female in "B", and removal of partition between "B" and "C". 6. Place of nest made by female in a circular aquarium evenly illuminated. 7. Place of second nest in circular aquarium after the placing of a light and a black card on either side of the aquarium. See text for discussion.

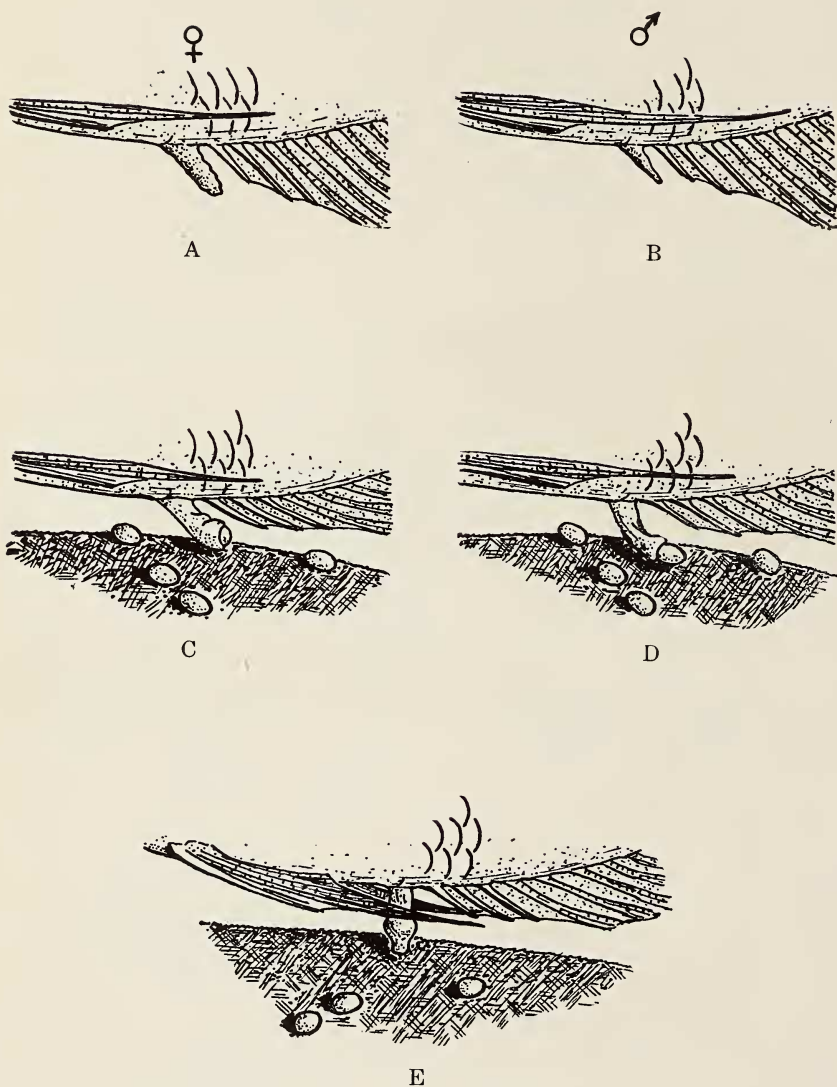


Fig. 2.—Egg laying of *Aequidens*. A. Female ovipositor. B. Male fertilizing organ. C. Female dragging ovipositor, with egg nearly extruded. D. The passage of the egg. E. The female assisting the passage of an egg by means of the ventral fins. See text for details. In all, the organs are slightly exaggerated in size.

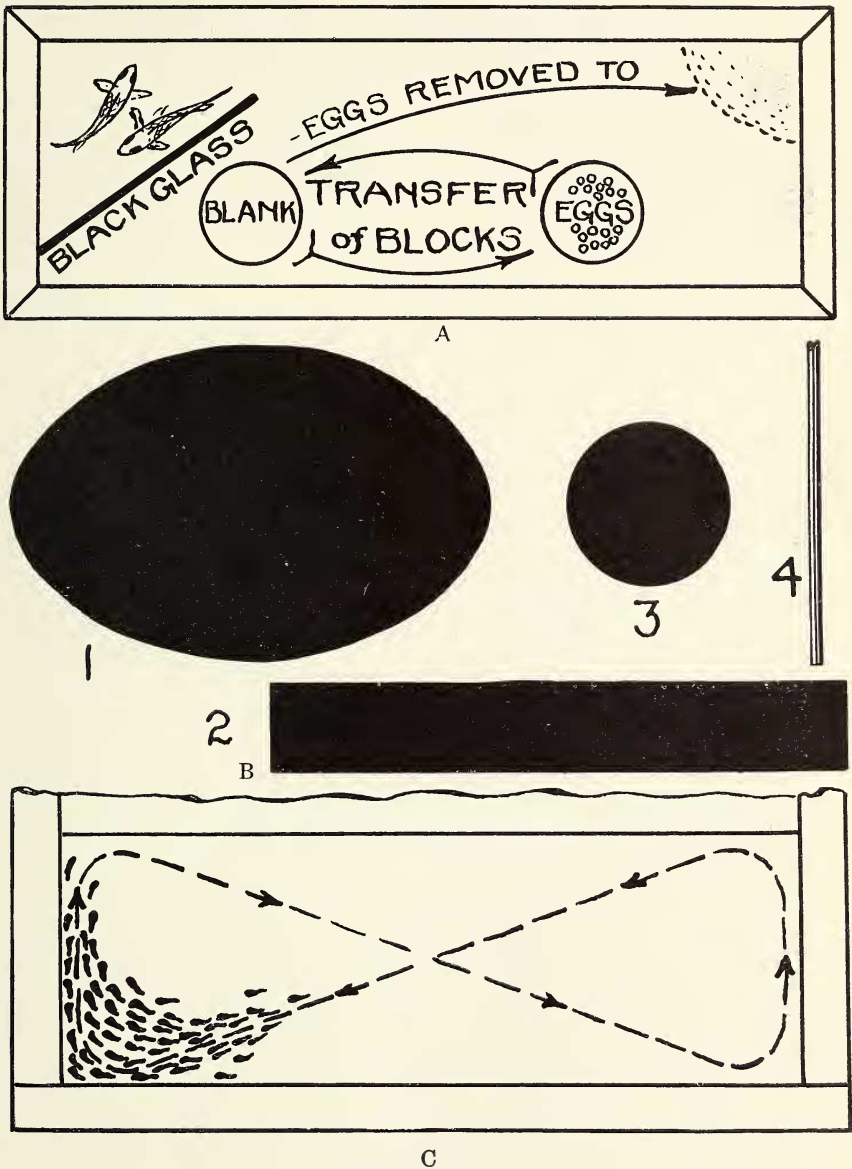


Fig. 3.—A. Diagram of method employed in shifting the eggs laid on an especially made cement block in such a fashion that the parents could not see the action. See text for explanatory discussion. B. Diagram of objects used in the study of tropisms of juvenile *Aequidens*. Items 1, 2 and 3 are black card targets, and 4 is the pale grey wire used for their support. C. Diagram of streaming movements of young fish in a small aquarium.



Fig. 4.—A typical pair of adult *Aequidens latifrons*, the parents of the fishes on which this study was based. Male, left; female, right.

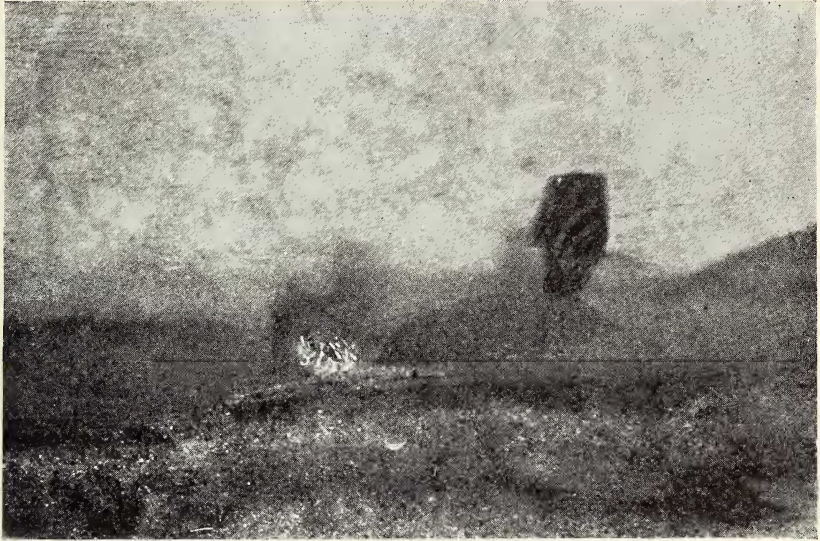
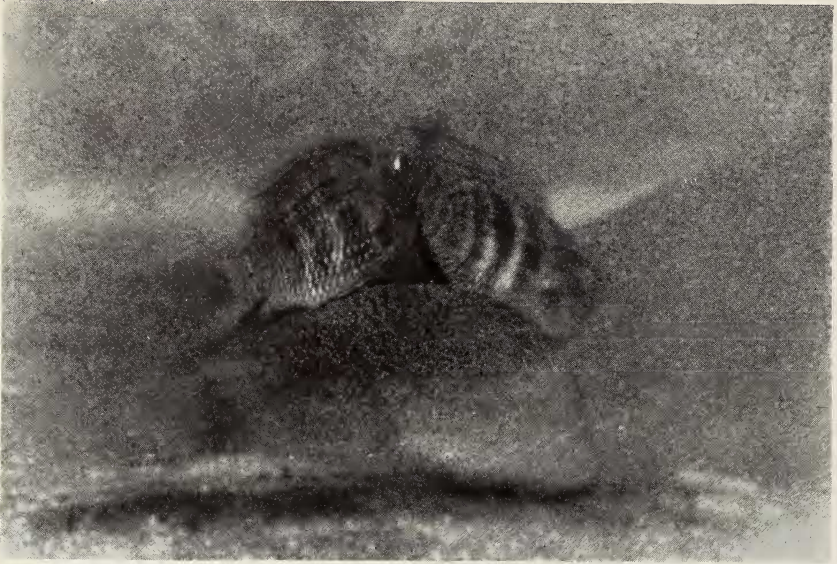


Fig. 5.—Two typical postures of *Aequidens* in spawning. The male to the left in both cases.



A

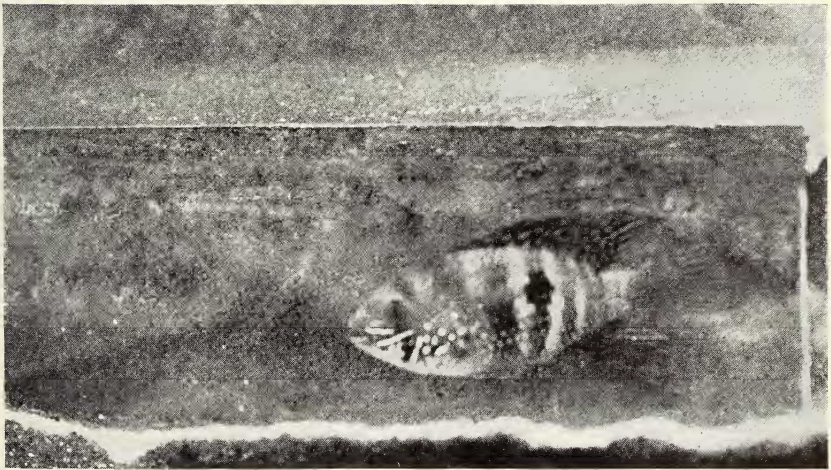


B

Fig. 6.—A. *Aequidens* near the end of a spawning. Male, right; female, left. B. Male *Aequidens* fanning water over eggs, with female approaching to relieve him. Note how the bottom has been cleared of detritus in the vicinity of the nest.

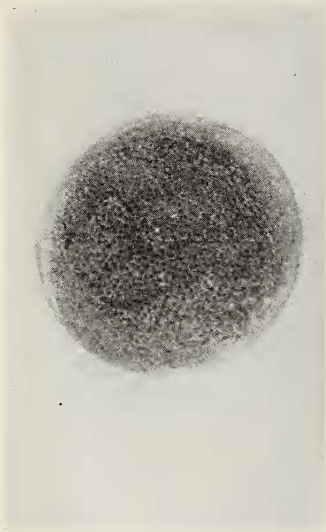


A

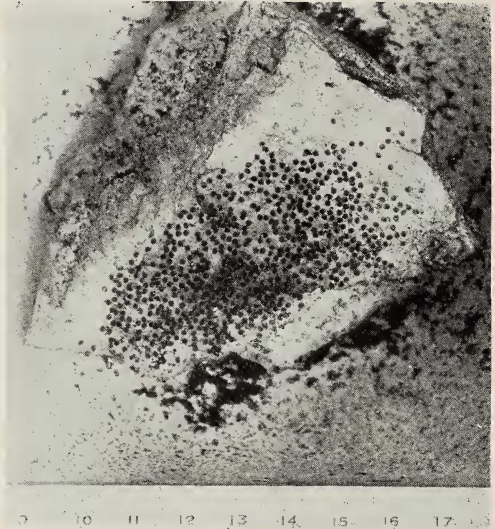


B

Fig. 7.—A. Eggs on the top of the cement block. B. Eggs on the side of the cement block.



A



B

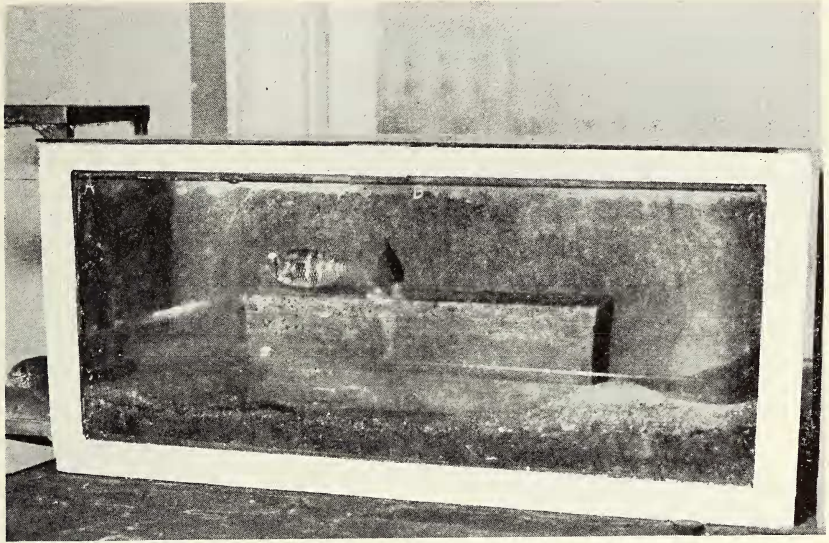


C

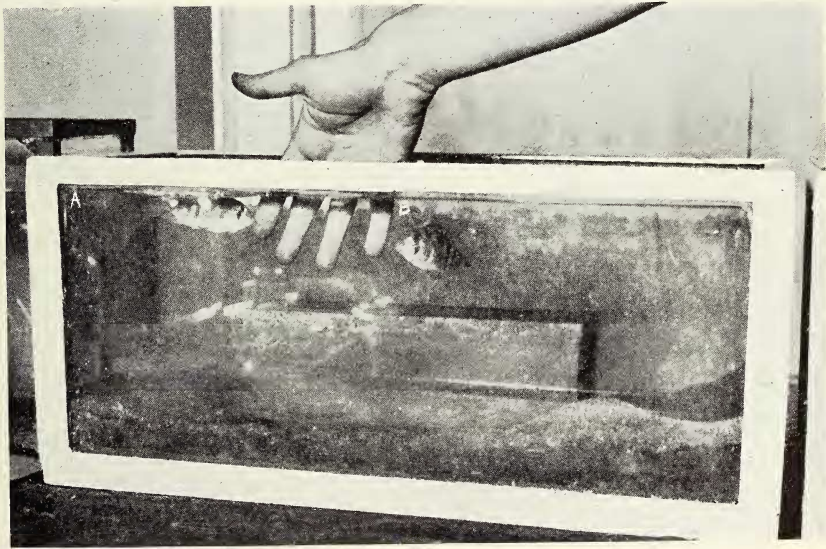


D

Fig. 8.—A. Eggs on a round cement block. B. Eggs on a white rock. C. Eggs on a black glass. D. The newly hatched young on the white rock shown in "B".

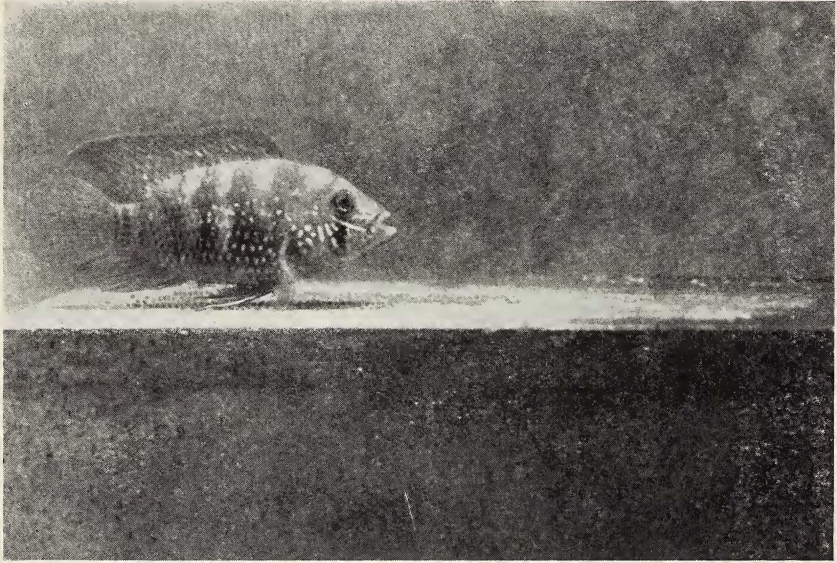


A

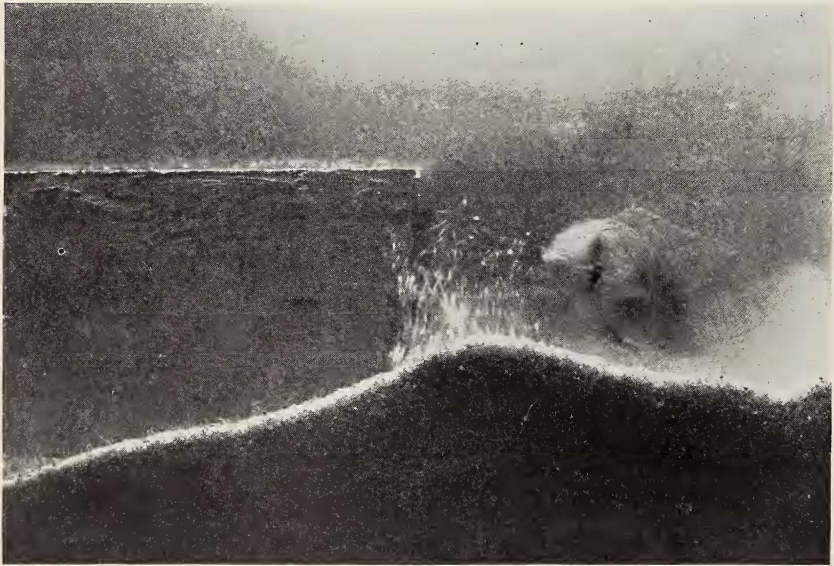


B

Fig. 9.—A. Both male and female incubating simultaneously. B. The same pair defending their eggs against an intruding hand.



A

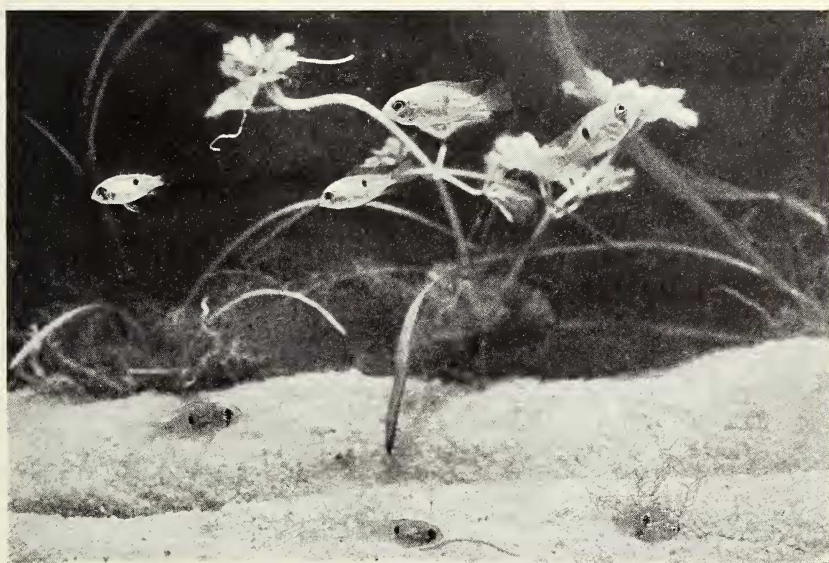


B

Fig. 10.—A. The male of Fig. 9 incubating and wiping the eggs with his ventral fins. B. The female of Fig. 9 excavating a hole for the reception of the young about to hatch. The sand grains ejected from the female's mouth have struck the glass wall and are falling.

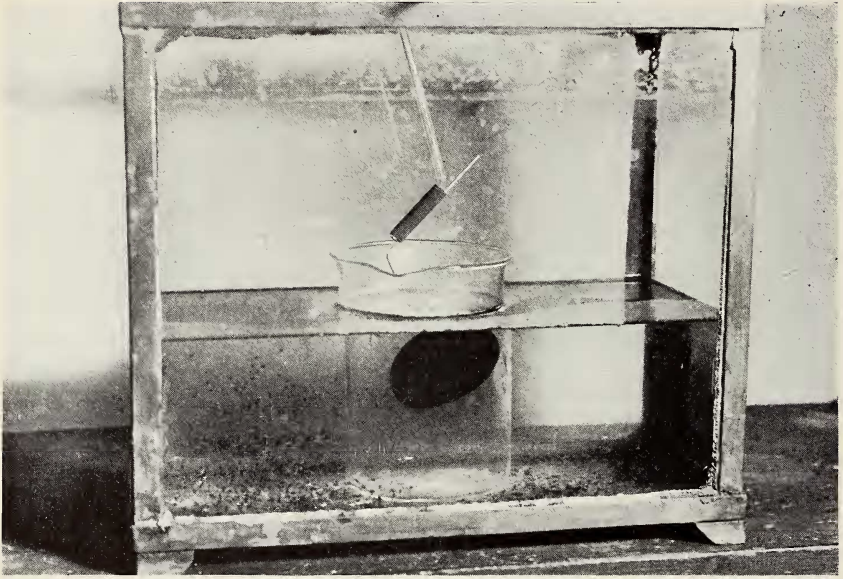


A

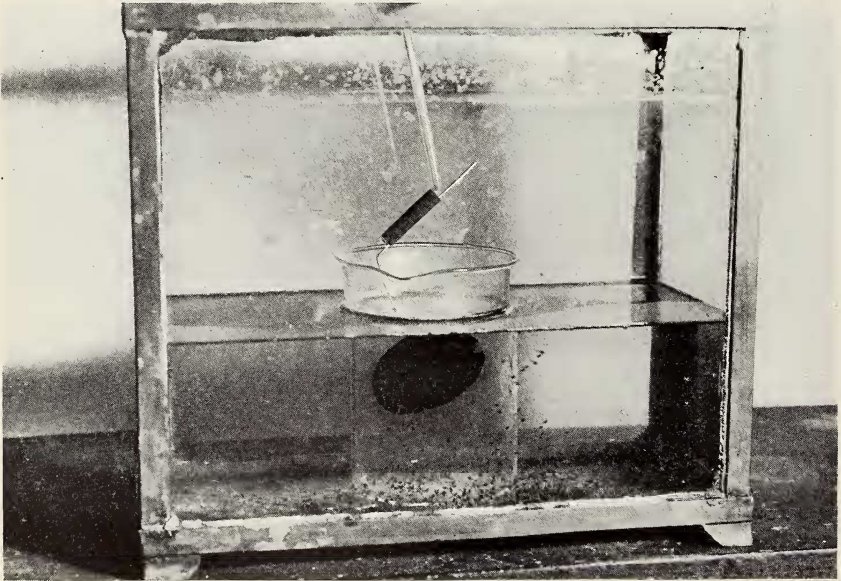


B

Fig. 11.—A. A male *Aequidens* gathering adventurous young, to return them to the brood shown in the background. B. Young *Aequidens* at the stage that they usually begin to escape from parental solicitude.

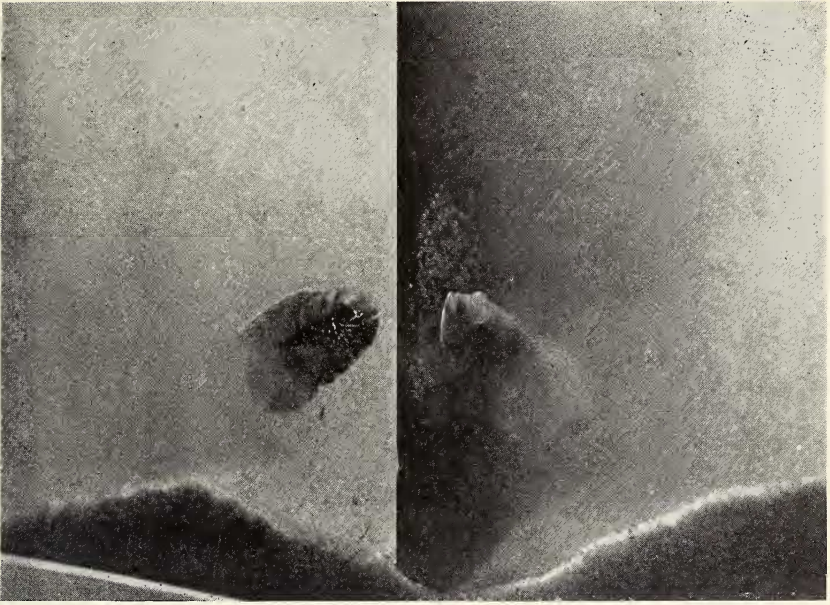


A

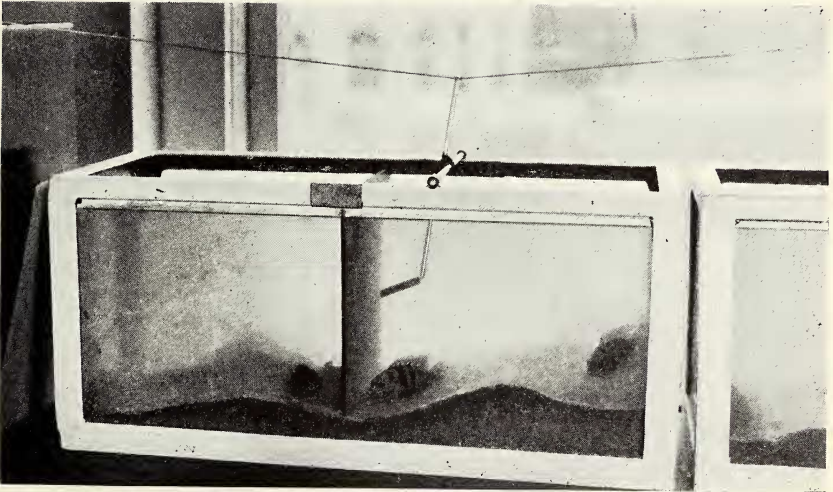


B

Fig. 12.—Reactions of juvenile *Aequidens* to a moving dark object in relation to their negative heliotropism. A. Young fish at end of tank farthest from light before oval target was moved. B. Young fish about beaker containing target after it had been oscillated a few times.

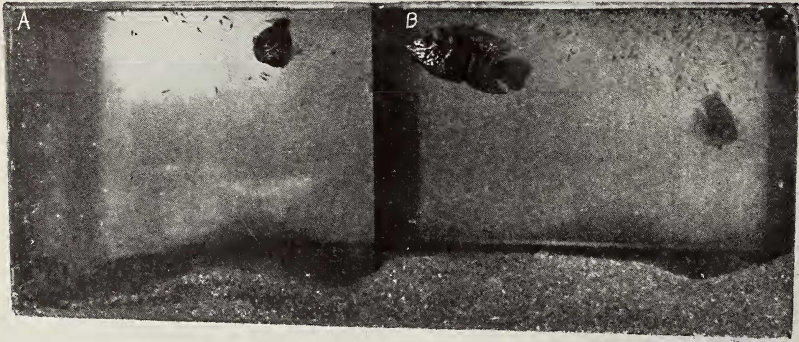


A



B

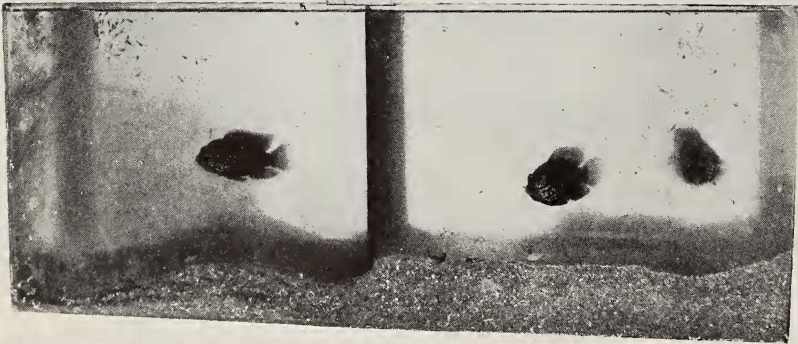
Fig. 13.—A. *Aequidens* fanning eggs on a black glass aquarium partition, and the peculiarly interested lone male on the other side of the partition. These eggs are the same as those shown in Figure 8C. B. Aquaria "A" and "B" of Figure 1 showing the tapping device.



A



B



C

Fig. 14.—A. A lone male *Aequidens* in the process of robbing the parents of their brood. (Center) At the start, with only a few obtained. B. and C. Later, when the lone male actually had more young than the parents.